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LATITUDINAL VARIATION IN THE DEFINITIVE PREBASIC MOLT OF YELLOW WARBLERS

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ABSTRACT.—We compared the definitive prebasic molt schedules of Yellow Warblers (*Dendroica petechia*) at two northern temperate breeding sites: the Vermont Institute of Natural Science (Vermont) in Woodstock, Vermont, and North Point (James Bay) on the southwestern coast of James Bay, Ontario. The two sites are separated by 8° of latitude. Yellow Warblers initiated molt significantly earlier in Vermont than at James Bay, with respective mean onset dates of 29 June and 20 July, but durations and rates of molt did not differ significantly between populations at the two sites. Mean individual molt durations spanned 44.5 days in Vermont and 40.0 days at James Bay. Molt rate of females differed significantly between the two sites, but male rates were similar. Based on number of primaries growing simultaneously, Yellow Warblers in both Vermont and James Bay appear to undergo a rapid and intense molt. The earlier and slightly more protracted molt of Yellow Warblers in Vermont may result from their earlier spring arrival and longer breeding season. *Received 22 November 2002, accepted 11 March 2003.*

Migratory birds that breed in seasonally variable environments typically partition reproduction, molt, and migration within their annual cycles. Energy resource conflicts are minimized by the temporal segregation of such events (Kendeigh 1949, Farner 1964, Bancroft and Woolfenden 1982). At temperate and northern latitudes, energetic constraints may become heightened by a shortened breeding season and the costs of migration. Several migratory passerine species overlap breeding with the definitive prebasic molt (Haukioja 1971, Green and Summers 1975, Rimmer 1988, Jenni and Winkler 1994, Hemborg et al. 1998). Molt and migration overlap appears to be less common (King 1974; but see Dolink and Blyumenthal 1967, Newton 1968, Cherry 1985, Rimmer 1988, Hahn et al. 1992), presumably because of the conflicting energetic and aerodynamic demands of both activities.

Few published molt studies exist for discrete breeding populations of North American wood-warblers (Parulinae) from northern temperate latitudes. Particularly lacking are data on the precise scheduling of reproduction, molt, and migration of known-identity breeders (but see Rimmer 1988). Although differences in the timing of prebasic molt between latitudinally separated populations of other passerine groups have been reported (Mewaldt and King 1978, Mulvihill and Rimmer 1997, Heise and Rimmer 2000), there are no published data for any wood-warbler species. Yellow Warblers (*Dendroica petechia*) breeding at northern latitudes undergo a rapid, intense molt that regularly overlaps the end of nesting and the beginning of southward migration (Rimmer 1988). This molt regime appears to be dictated by a late spring arrival, coupled with deteriorating food supplies and the onset of early cold weather in late summer. In this paper, we compare data collected at a central Vermont breeding site with those previously published from the James Bay coast, in order to examine latitudinal variation in the prebasic molt schedules of adult Yellow Warblers.

STUDY AREA AND METHODS

We collected molt data during the summers of 1986–2000 at the Vermont Inst. of Natural Science (hereafter "Vermont") in Woodstock, Vermont (43° 36′ N, 72° 32′ W) and from 1980–1984 at North Point (hereafter "James Bay") on the southwestern coast of James Bay, Ontario (51° 29′ N, 80° 27′ W). The two sites are separated by a straight-line distance of 1,030 km. For descriptions of the James Bay site and data collection methods, see Rimmer (1988). We collected molt data in Vermont on a 3-ha site characterized by second growth deciduous shrub-woodland, consisting of brushy thickets interspersed with stands of mostly mature trees 10–20 m in height. Dominant canopy species included

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sugar maple (*Acer saccharum*), quaking aspen (*Populus tremuloides*), black cherry (*Prunus serotina*), and white ash (*Fraxinus americana*); dominant shrubs included willow (*Salix* spp.), autumn olive (*Elaeagnus umbellata*), steeplebush (*Spiraea communis*), and common buckthorn (*Rhamnus cathartica*). From 1986–2000, we operated 19–21 mist nets (12 × 2.6 m, 36-mm mesh) 1–3 days/week during July and 5 days/week from 1 August to early November. Nets were opened for 6 h/day, beginning 0.5 h before sunrise, except during adverse weather conditions.

We banded all captured individuals with USFWS aluminum leg bands. We aged Yellow Warblers as either second year (SY) or after second year (ASY), according to criteria in Pyle et al. (1997). When individuals did not fit clearly into either age category, they were designated as after hatching year (AHY). Males and females were distinguishable in all plumages and at all stages of molt.

We used a conventional molt scoring system (Ashmole 1962, Newton 1966) which assigns each remex and rectrix a score of 0 to 5 as follows: 0 = not dropped, 1 = missing or in pin, 2 = "brush" stage to one-third grown, 3 = one-third to two-thirds grown, 4 = two-thirds to full-grown but with waxy sheath remaining, 5 = completely regrown. We followed Bancroft and Woolfenden (1982) in obtaining a remigial score for all 18 primary feathers and both the left and right sixth secondary. This remigial score results in a more linear relationship of molt score to date than by using primary score alone (Bancroft and Woolfenden 1982). The assumption of linearity between molt score and date is important if recapture data and regression analysis are used to estimate rate and duration of molt (Newton 1966, Bancroft and Woolfenden 1982, Rimmer 1988). A remigial score of 0 indicates that remigial molt had not begun, while a score of 100 indicates completion of this molt.

We examined remigial molt on the assumption that its duration provides an accurate index of the period during which a bird's entire plumage is replaced (Bancroft and Woolfenden 1982, Rimmer 1988). We estimated the duration of prebasic molt, based on the rate of remex molt, in two ways: (1) using linear regression analysis of remigial scores versus date for all individuals in active remigial molt, and (2) from individuals captured two or more times in the same molt cycle with a minimum of five days between captures. However, regression analysis underestimates molt rate when molt onset is highly asynchronous within a population (Pimm 1976, Bancroft and Woolfenden 1982, Rimmer 1988). Due to the asynchronous onset of molt in Vermont birds, we used only recapture data in our statistical analyses, although we present regression results for comparative purposes.

In calculating individual molt rates, we used only first and last captures. For these individuals, we calculated rates of molt by dividing the difference in remigial score by the number of days between captures. Because rates of molt decrease late in the molt cycle of Yellow Warblers (Rimmer 1988), we used only birds whose initial remigial score was <85. Rate calculations are expressed as points/day. We calculated dates of molt onset for individuals and the sampled population by extrapolating rates from recaptured birds.

RESULTS

Sequence, rate, and duration of molt.—The sequence of remex and rectrix molt in Yellow Warblers in Vermont closely matched that of birds examined at James Bay (Rimmer 1988). The innermost primary invariably was the first flight feather to drop, and primaries were replaced in descending order, proximal to distal. The outermost secondary usually began molting simultaneously with primary 6 or 7, and secondaries 1–6 were replaced distal to proximal. Secondary 6 typically was the last remex to complete growth.

We calculated the remex molt rate of 13 Vermont individuals caught more than once during the same remigial molt cycle (Fig. 1). The mean molt rate of females did not differ significantly from that of males (Table 1; $t_{11} = 0.003$, $P = 0.99$). Small sample sizes of known-aged birds precluded age-related molt analyses (Table 1).

Vermont males ($n = 7$) completed remigial molt during a mean of 45 days ± 5.64 SD, females ($n = 6$) during 44 days ± 5.86 SD. Remex molt rates of males ranged from 1.61–3.00 points/day, while females molted at rates between 1.00 and 3.05 points/day. The greatest deviations from mean molt rates were ex-

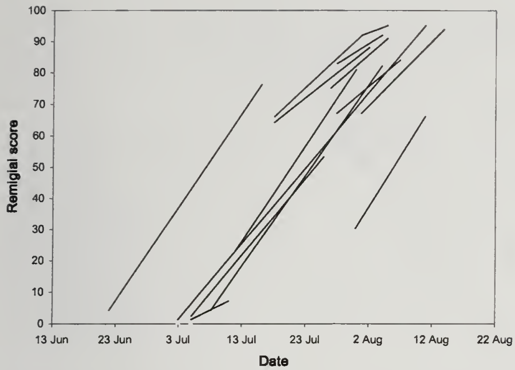

FIG. 1. Nearly parallel slopes of lines connecting remex scores of individual Yellow Warblers examined two or more times during the definitive prebasic molt in Vermont, 1986–2000, indicate that overall molt rates were similar among all birds.

hibited by individuals examined only early or late in the molt cycle or in which the interval between successive captures was short. Rates were slowest during the early and late stages of molt (Fig. 1), when fewer remiges were growing simultaneously. However, the similarity of mean molt rates between males and females and the nearly parallel slopes of the longest lines in Fig. 1 indicate that the overall molt rate was very similar among all Vermont birds, independent of initiation date.

For both male and female Yellow Warblers, molt rates did not differ significantly between Vermont and James Bay (females: $t^5 = 1.71$, $P = 0.14$; males: $t^9 = 0.63$, $P = 0.27$; Table 1). *Post hoc* power for different effect size (Johnson 1999) on differences in molt rates was 0.80 for females ($n = 19$) and 0.82 for males ($n = 17$), with an effect size of 1 for each. Molt durations reflected these small differences, with James Bay females completing molt in only 6 fewer days than Vermont females (44 versus 38 days), while James Bay males molted only 3 days more rapidly than Vermont birds (45 versus 42 days).

We evaluated the intensity of remigial molt by determining the maximum number of primaries growing simultaneously. This stage in the molt corresponded with remigial scores between 51 and 70. The mean number of simultaneously growing primaries during this period did not differ significantly between James Bay and Vermont Yellow Warblers (6.3 ± 0.85 SD and 5.2 ± 0.21 SD, respectively; $t^{12} = 1.85$, $P = 0.20$).

Chronology of molt.—We examined molting Yellow Warblers captured from late June to early September. The onset and termination of molt spanned 3-week periods between late June and mid-July and early to late August, respectively (Fig. 2). The mean molt onset date for all Yellow Warblers in Vermont was 29 June. Females began molting earlier than males, but the respective mean initiation dates of 27 June and 1 July did not differ significantly ($t^{11} = 0.75$, $P = 0.47$). The mean molt termination date for all Vermont birds was 12 August. Females completed molt on 10 August, 5 days earlier than the mean male termination date of 15 August. This difference also was not significant ($t^{11} = 1.28$, $P = 0.23$).

Overall, Yellow Warblers in Vermont began and ended prebasic molt 21 days earlier than the birds at James Bay (Table 2). Molt onset dates for Vermont males were significantly earlier than for James Bay birds ($t^{15} = 4.08$, $P = 0.001$), and Vermont females initiated molt significantly earlier than did females at James Bay ($t^{18} = 8.53$, $P < 0.0001$). Mean molt termination dates of Vermont males and females also were significantly earlier than those of James Bay birds (males: $t^{13} = 4.14$, $P = 0.001$; females: $t^{18} = 4.79$, $P = 0.0001$).

TABLE 1. Male and female Yellow Warbler molt rates from Vermont (VT) and James Bay, Ontario (JB), based on recapture data and linear regression.

	Recapture			Regression		
Class	*n*	Rate[a]	SD	*n*	Rate[a]	SD
Males-VT	7	2.142	0.657	44	1.831	0.191
Males-JB	10	2.313	0.368	94	2.178	0.093
Females-VT	6	2.140	0.821	31	2.191	0.365
Females-JB	13	2.704	0.260	123	2.384	0.097

[a] Change in remex score per day (see Methods).

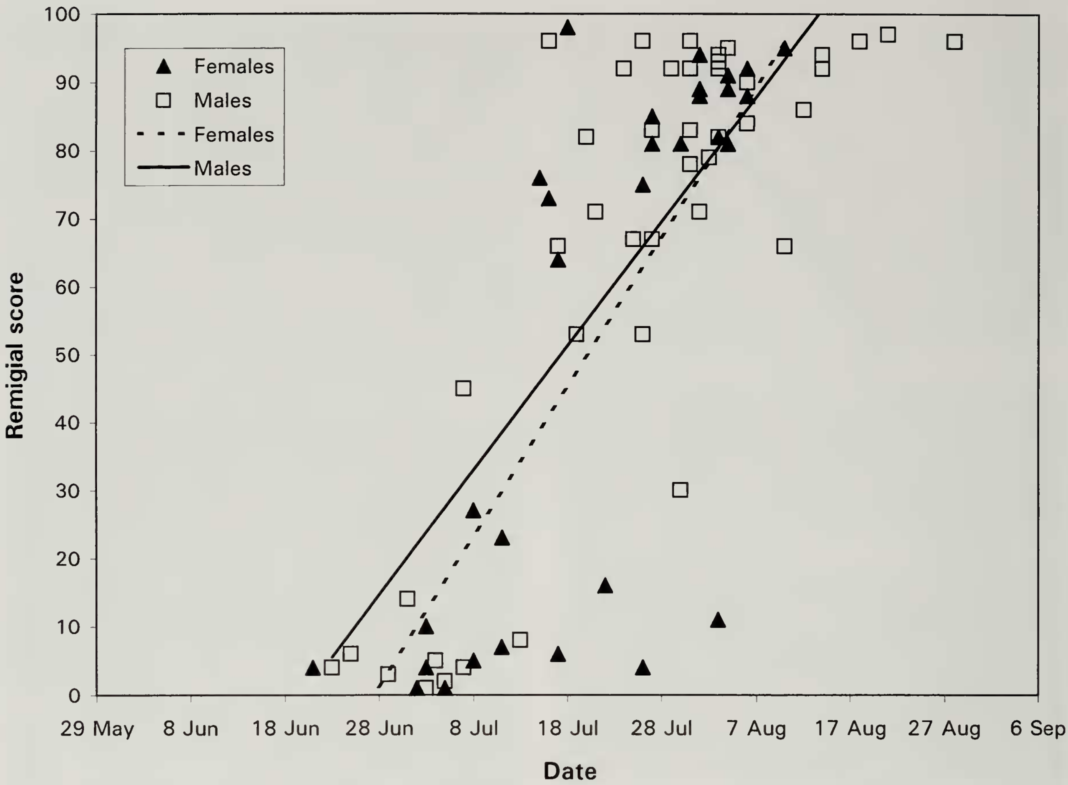

FIG. 2. Remex scores of Yellow Warblers examined during the definitive prebasic molt in Vermont, 1986–2000, show that onset and termination dates spanned 3-week periods between late June and mid-July and early to late August, respectively.

Molt and migration.—Although we could not reliably distinguish between local and transient birds in our mist net samples, we examined the integration of molt and migration under the assumption that most unbanded Yellow Warblers captured after 15 July were nonlocal birds (Laughlin and Kibbe 1985). The dates of capture for unbanded adults and immatures after 15 July were similar; mean capture date for adults (n = 30) was 6 August ± 16.5 days, mean capture date for immatures (n = 66) was 4 August ± 14.2 days. We recaptured four adults examined both in early or mid-molt and in nearly complete basic plumage, indicating that these individuals had completed remigial molt at our study site.

DISCUSSION

Yellow Warblers in Vermont required a mean of 44.5 days to complete remigial molt, 4.5 days longer than the mean molt duration (40.0 days) at North Point. Typically, migratory passerines breeding at northern temperate latitudes undergo a more rapid molt than sympatric, nonmigratory populations and species, or those breeding farther south (Dolnik and Blyumenthal 1967, Evans et al. 1967, Morton et al. 1969, Haukioja 1971, Mewaldt and King 1978). The molt durations of Yellow Warblers are considerably shorter than those reported for two other temperate wood-warbler species (Foster 1967, Nolan 1978), although precise data of individuals are lacking in those studies. Black-and-white Warblers (*Mniotilta varia*) breeding at two widely separated latitudes (New England and James Bay) showed similar mean durations of 45 days in both areas (T. Lloyd-Evans and CCR unpubl. data). Because few comparable molt data exist among the Parulidae, however, there is little basis for evaluating the prebasic molt patterns of Vermont Yellow Warblers with respect to other members of this family.

Yellow Warblers breeding in Vermont begin

TABLE 2. Estimated molt onset and termination dates for recaptured Yellow Warblers from Vermont (VT) and James Bay, Ontario (JB).

Class	*n*	Molt onset		Molt termination	
		Date	SD[a]	Date	SD[a]
Males-VT	7	1 July	±10.0	15 August	±5.9
Males-JB	10	17 July	±6.7	28 August	±7.7
Females-VINS	6	27 June	±7.5	10 August	±9.1
Females-JB	13	22 July	±5.3	28 August	±7.7
All Birds-VT	13	29 June	±8.7	12 August	±7.7
All Birds-JB	23	20 July	±6.3	28 August	±7.2

[a] Number of days.

and finish the remigial molt 2–3 weeks earlier than birds at northern latitudes. Both males and females exhibited this pattern. There are approximately 8° of latitude between Vermont and North Point, corresponding to a delay in molt onset of 1.8–2.6 days/degree northward. This difference is higher than the 0.4–1.0 days/degree for Chaffinches (*Fringilla coelebs*; Noskov 1975), but is similar to that reported for White-crowned Sparrows (*Zonotrichia leucophrys*, 2.6 days/degree; Mewaldt and King 1978). Both male and female Black-and-white Warblers in New England molted 13–14 days earlier than the same sex at North Point, presumably reflecting an earlier spring arrival and an earlier breeding season in the south (T. Lloyd-Evans and CCR unpubl. data). The mean known fledging date of five Yellow Warbler nests at Woodstock was 21 June (CCR unpubl. data), three weeks earlier than the mean fledging date of 11–12 July at North Point (Rimmer 1988). Thus, the earlier breeding chronology of the southern population appears to dictate, at least in part, its earlier molt schedule.

Passerine molt studies at northern temperate latitudes have shown that males tend to begin molting earlier than females (Mewaldt and King 1978, Tianen 1981, Rimmer 1988). Other studies at lower latitudes have found no significant sexual differences in molt onset (Newton 1966, Snow 1969, Nolan 1978, Heise and Rimmer 2000). Yellow Warblers appear to follow this pattern, as James Bay males initiate molt significantly earlier (5–7 days) than females (Rimmer 1988), but both sexes initiate molt on similar dates in Vermont. Rimmer (1988) suggested that a delayed molt onset in North Point females might result from their physiological inability to initiate molt as early as males, due to more pronounced energetic constraints caused by nest construction, egg synthesis, incubation, brooding, and nestling feeding duties during a relatively short summer. The earlier and more protracted breeding season of Vermont females may impose fewer such constraints and enable their relatively earlier initiation of molt.

While both sexes of Yellow Warblers in northern Ontario molted more rapidly than respective Vermont birds, differences were slight. The lack of significant geographic difference in molt rates may have resulted from low statistical power associated with small sample sizes and small effects. The result is particularly surprising for females, given likely differences in ecological and physiological constraints facing birds at the two localities. A relatively more rapid molt in James Bay females might be expected in order to compensate for their delayed start in the face of selective pressures to migrate as early as possible due to diminishing late summer insect food resources. The lower rate of molt of James Bay males relative to James Bay females may have resulted in part from the males' earlier onset, enabling them to avoid the costs of a rapid molt, and from the males' relatively higher energy expenditure during molt, since many continued to sing and apparently maintained territories until their southward departure (Rimmer 1988).

Despite a latitudinal difference of 8° between James Bay and Vermont, Yellow Warblers at the northern site molted only 4.5 days faster than their southern counterparts. This difference seems surprisingly small if ecological constraints at the two sites are driving respective molt schedules. A more protracted molt would seem to be the optimal pattern for a bird facing relatively fewer constraints on its time and energy, as has been shown in sedentary passerines at high elevations (Pitelka 1958, Newton 1966, Orell and Ojanen 1980; Common Redpolls, *Carduelis flammea*, at James Bay, CCR unpubl. data), wintering Palearctic warblers (Pearson 1973, Price 1981), and resident versus migrant shorebird populations (Pienkowski et al. 1976). With an earlier, more prolonged breeding season and a more extended period of arthropod prey abundance in Vermont (CCR unpubl. data), Vermont Yellow Warblers might be expected to undergo a less rapid and intense molt than the 44.5 days we documented. However, individual Vermont birds, particularly females that we examined during the peak of the remigial molt, showed wing gaps nearly as large as those of North Point birds, and they may have been similarly incapable of sustained flight (Rimmer 1988). This suggests that both populations experience strong selective pressure to compress their prebasic molt. The energetic costs of a rapid molt, such as decreased thermoregulatory abilities and reduced flight efficiency, combined with the need to prepare physiologically for the impending long-distance migration, may impose an upper limit on the molt rate of James Bay Yellow Warblers and prevent further acceleration.

It is unclear from our data whether or not adult Yellow Warblers in Vermont regularly migrated before completing their prebasic molt. Based on four recaptured individuals examined at the beginning and end of molt, we believe that Vermont birds complete remigial molt on the breeding grounds. Although many Yellow Warblers appear to depart Vermont in late July (Laughlin and Kibbe 1985), well before the mean molt termination date of Vermont birds, several studies have documented that breeding area departures do not necessarily indicate migration onset (Nolan 1978, Rimmer 1988, Rappole and Ballard 1987, Vega Rivera et al. 1998). At James Bay, most male Yellow Warblers remained on breeding territories throughout the summer and departed during the late stages of remigial molt, while females showed comparatively little postbreeding site attachment and appeared to undergo a molt dispersal (Rimmer 1988).

Throughout their eastern North American breeding range, Yellow Warblers are among the earliest wood-warblers to undergo fall migration (Laughlin and Kibbe 1985, Veit and Petersen 1993, Bull 1998, Lowther et al. 1999); southern populations appear to depart earlier than those in the north (Lowther et al. 1999). Arrivals on Mexican wintering grounds begin in late July, mid- to late August in southern Central America (Lowther et al. 1999). Yellow Warblers are strongly territorial during winter, particularly toward members of other small, insectivorous species, suggesting that intense interspecific competition for rich arthropod food resources occurs (Greenberg and Salgado-Ortiz 1994). Under the assumption that high quality winter habitats are limiting for many species of long-distance migrants and that occupancy of optimal winter habitats enhances overall fitness (Marra et al. 1998), early-arriving Yellow Warblers may gain an important selective advantage. Both intra- and interspecific habitat competition may be involved if Yellow Warblers from different breeding localities are in contact on the wintering grounds, as has been shown for other species (Chamberlain et al. 1997, Hobson and Wassenaar 1997, Hobson et al. 2001). Selection for early arrival on the wintering grounds has been suggested for several species of *Sylvia* warblers breeding in Europe (Fransson 1995, Hall and Fransson 2001). For birds breeding at more southern latitudes such as Vermont, the aerodynamic and energetic costs of a rapid molt may be outweighed by the benefits of a relatively early southward departure and winter arrival. Northern populations such as those at James Bay may be unable to further advance or accelerate their molt, due to the ecological constraints of a high-latitude summer (Jenni and Winkler 1994, Hemborg et al. 1998). We believe that the unexpected compression of prebasic molt in Vermont Yellow Warblers may be an adaptive response more to resource competition on the wintering grounds, mediated through fall migration schedules, than to latitudinal and ecological differences between Vermont and James Bay.

The apparent selective pressures for a rapid molt in Yellow Warblers beg the question of why this and most other Nearctic-Neotropical migrant passerines have not evolved the seasonally divided molt strategies typical of many long-distance Palearctic migrants (Alerstam and Högstedt 1982, Jenni and Winkler 1994, Holmgren and Hedenström 1995). By suspending prebasic molt, or postponing it entirely until arrival on their wintering grounds, Yellow Warblers theoretically could minimize their energetic costs while maximizing the benefits of early arrival on the wintering grounds. One possible explanation is simply that molt patterns are phylogenetically constrained, thus limiting the scope of adaptive responses. Conversely, arrival on the wintering grounds with a new set of high quality feathers might enhance survival (Holmgren and Hedenström 1995) through competitive advantages in territory acquisition and maintenance, thus promoting an earlier and/or more rapid postbreeding molt. Few empirical data exist to test such hypotheses in Yellow Warblers or other migrant passerines. A comprehensive review of passerine molt patterns across phylogenetic lines and life history strategies is needed to better elucidate the evolutionary mechanisms that shape the integration of molt into avian annual cycles (but see Svensson and Hedenström 1999).

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